"After a patient search the source of the signal was located. But was she alive? Telemetry pulses still suggested near-ambient temperature. Perhaps the animal was alive and in torpor?"

ECHIDNAS IN THE HIGH COUNTRY

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OF ALL AUSTRALIA'S 150 OR SO native mammals, only the Short-beaked Echidnas (*Tachyglossus aculeatus)* have a distribution that can be said to be Australia-wide. They are found in deserts, wet and dry sclerophyll forests, rainforests and heathlands. They are even seen in the high country of the Australian Alps.

This remarkable range of habitats does not fit well with the usual stereotype of Echidnas as primitive, egg-laying hold-overs from the earliest days of mammalian evolution. One would expect a living fossil to survive only in an isolated habitat to which it was specifically adapted. To

Gordon Grigg locates the antenna wire, which provides a clue to the position of the recording box used to track Echidnas in the high country. Above: tell-tale signs of an Echidna– fresh tracks in the snow.

LYN BEARD

be widespread and even common in such a diversity of habitats must require a great range of physiological and behavioural skills. We wondered if their secret was advanced adaptation or primitive plasticity.

In the traditional manner of comparative zoologists, we decided to approach a general question by looking at an extreme. The Australian Alps, above the snowline, provide an extreme habitat, and we knew that Echidnas could be found there. Cross-country ski enthusiasts told us of seeing Echidnas out and about in the middle of winter, poking about in the snow, and there was even a reliable report of one within a few metres of the summit of Mt Kosciusko. Such observations might be considered a bit unusual for a fox or a possum, but they begged further investigation for an animal often accused of 'primitive thermoregulation', 'heterothermy' and 'incomplete homeothermy'.

Of course one explanation for such sightings could be that the individual Echidnas were outside their normal winter range, perhaps stranded at higher altitudes to which they had wandered during the warmer months. Alternatively Echidnas might live there year round, spending the winter under the snow and emerging from time to time, a pattern reminiscent of mammalian hibernators. But they couldn't do that! One of us (M. Augee) had frequently stated that Echidnas are *not* hibernators. It was there in black-and-white, in scientific journals. That conclusion had been reached because captive Echidnas would only enter torpor reluctantly. In early studies carried out at Sydney University by H. Wardlaw in 1915, most Echidnas that did enter torpor died. Besides, the mating season is usually stated to be in July–August (mid winter), a most inconvenient time to be in hibernation! There were a few anecdotal reports of Echidnas found in a lethargic state in the wild during winter (one reported to have been dug out by earth-moving equipment), but no field data where actual body temperatures had been measured. We felt that the only convincing data would be that collected in the field; and the only way to collect such data would be by radio-tracking (see box).

So we applied to the Australian Research Council for funds to solve the puzzle. In preparing this application we found very little in the literature about the biology of Echidnas in the field. The lack of field studies is probably related to the difficulty of relocating Echidnas and the impossibility of trapping them. The obvious technique to use was telemetry, employing modern, implantable, long-lived, temperature-sensitive transmitters that are small enough to be easily tolerated by an animal the size of an Echidna.

But first to find some Echidnas in the alpine habitat. We put out the word amongst the staff of Kosciusko National Park (KNP) that we particularly wanted animals from the highest ridges, as well as a 'control' group lower down in the Waste Point or Jindabyne area below the snowline. Meanwhile the grant had been obtained and laboratory work began at Sydney University, with Grigg and Beard perfecting the techniques of implanting transmitters within the peritoneal (body) cavity. Whenever possible we went to KNP in the hope of finding Echidnas ourselves.

As luck would have it, the very first animal that turned up in KNP was in a perfect spot for the study. Early in 1987 John Whittaker, while delivering ski-trail poles to Prussian Plain at 1,720 metres elevation on the crest of Ramshead Range south-west of Perisher, captured a tan-coloured female weighing about three kilograms. We implanted a transmitter and released her at the exact site of capture. The weather was warm as she crawled out of the opened sack and took a couple of hesitant steps onto the snowgrass. After sniffing the air she hastily burrowed into the soft earth. Although designated E10 (Echidna number ten), this was the first animal released in the Kosciusko study area.

Over the next few weeks we plotted the position and monitored the body temperature of E10 as she moved about Prussian Plain. We were pleased that she remained there and did not head down into one of the valleys. By now we also

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Body Temperature by Radiotelemetry

By surgically implanting a small temperature-sensitive radio transmitter into the body cavity of an animal it is relatively easy to keep tabs on them for months, or even a couple of years, relocating them whenever required and recording body temperature without causing them any disturbance. This provides biologists with a powerful technique for learning about the behaviour and physiology of free-ranging animals.

The transmitters we use measure 20 × 8 × 7 millimetres. Powered by a three-volt lithium battery, they are waterproofed with a physiologically inert wax. Once powered up, pulses of 15 milliseconds duration are sent every second at 30° C, slowing down as temperature falls. The pulses are detected using a specially designed radio receiver. By careful calibration prior to implantation and careful timing of pulses once the animal is released, body temperatures can be monitored with an accuracy of ±0.2° C.

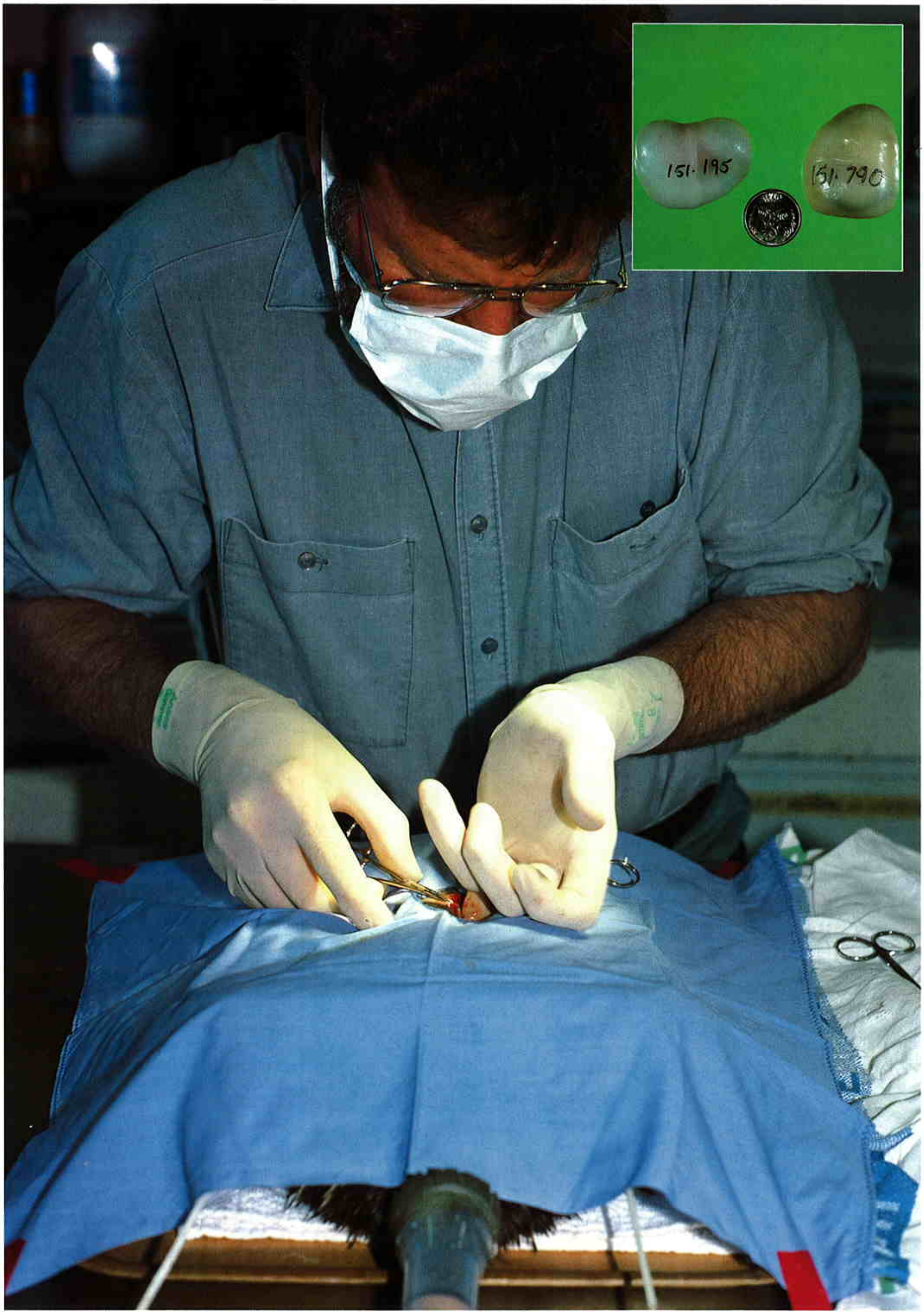
Each transmitter has a unique frequency that can be tuned in with the receiver. With a directional hand-held antenna connected to the receiver, an animal can be located by following the direction of greatest signal strength. The range is typically one kilometre, but often two to three kilometres.

To record body temperature when we could not be in the field, we devised a battery-operated system in which a programmable timer turned on the receiver and a tape-recorder at predetermined intervals. In this way we could sample temperatures hourly, eight-hourly, or whenever we wished, thereby covering intervals between field trips and obtaining a more or less continuous record of changes in body temperature for months at a time, changing the tape every two to three weeks as required. Using a scanner plugged into the receiver, the same 'box' could be made to record more than one individual's body temperature plus ambient temperature.

—L.A. Beard & G.C. Grigg

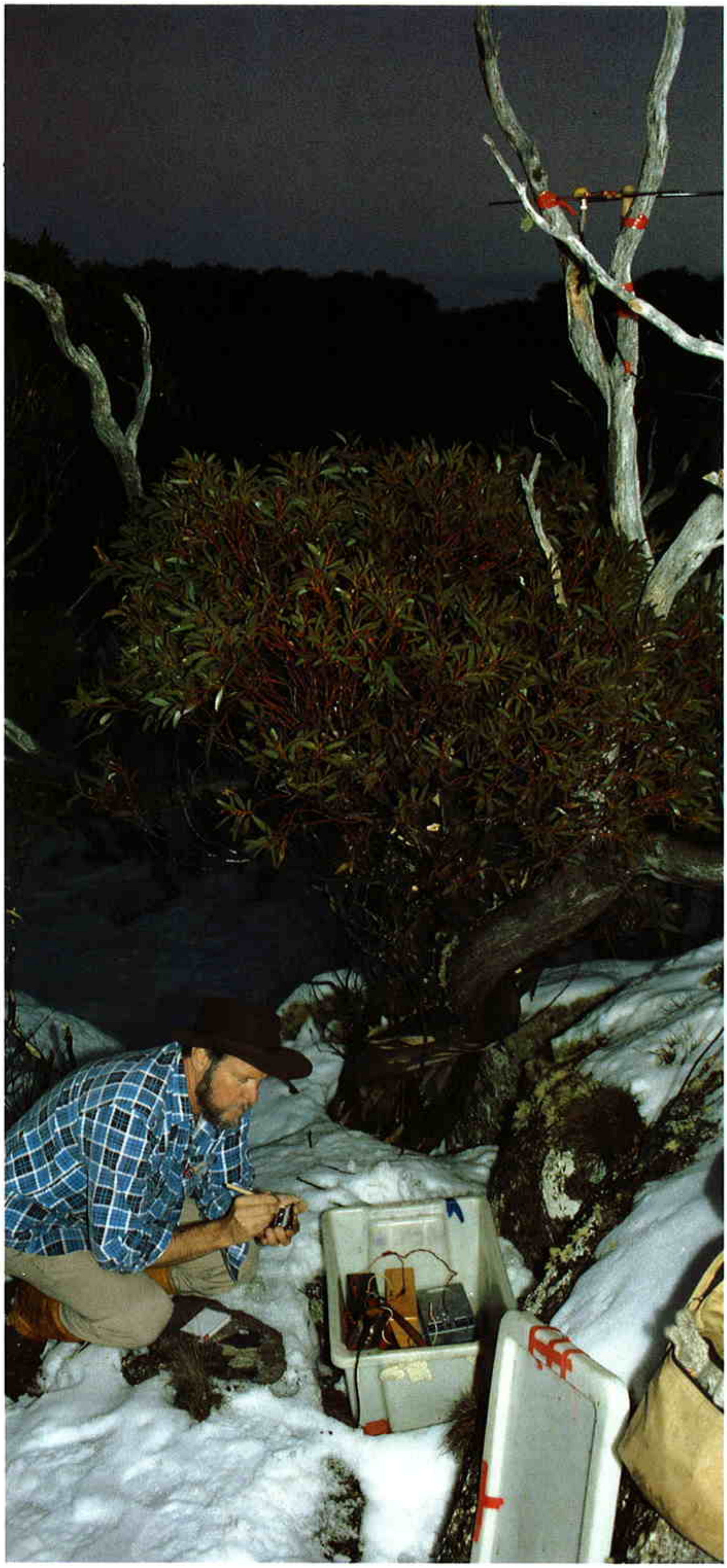
Using a stopwatch or digital processor, Lyn Beard reads off the pulse intervals between signals recorded on cassette tape from the transmittered animals every few hours for the past couple of weeks.

Transmitters are implanted intraperitoneally under sterile conditions, as approved by the university's Animal Care Committee. Inset: the transmitters are coated with a physiologically inert wax.



TOM GORRINGE

LYN BEARD


LYN BEARD

had two other Echidnas with transmitters (E11 and E13) at Waste Point on the shore of Lake Jindabyne (altitude 1,000 metres) and another (E15) at Rennix Gap (1,580 metres). We also came by a female (E12) from Dead Horse Gap, another high-altitude location, and released her onto Prussian Plain after implanting a transmitter. Now we had three animals above and two below the normal snowline, and were ready to establish the summer patterns of behaviour and body temperature before the weather turned cold.

IT WAS ALREADY KNOWN FROM STUDIES OF Echidnas in captivity that body temperatures vary on a daily basis, and we soon found this to be true in our summer field study. Most mammals have a small daily variation of a degree or so, being warmer when active and cooler when at rest. We found the Echidnas in KNP to vary daily by 6–8° C. The pattern set by E10 on Prussian Plain in those early weeks turned out to be typical. She was active all day, foraging for small black ants by digging along the edge of fallen timber and under clumps of snowgrass, with a body temperature of 32–34° C regardless of the weather. Soon after daylight had faded she would hole up for the night in a suitable retreat: a hollow log, under a rock, in a disused burrow or, as we observed several times, under a convenient clump of snowgrass. Shortly thereafter, as the lengthening times between pulses from the radio transmitter deep within her showed, body temperature began to fall, quite slowly, as she rested for the night. In these latitudes Echidnas tend to be late risers, avoiding the chill of early morning, so the minimal body temperatures at this time of year were measured between 9 and 10 am and were typically 25–27° C. When E10 emerged and became active again, body temperature rose rapidly; sometimes associated with basking in the sun but more certainly associated with heat produced from muscular activity. Sometimes, when Prussian Plain was swept with wind and rain, she would stay in her retreat and cool further for a day or two before re-emerging to forage and warm up, body temperature always returning to 32–34° C.

This was the typical pattern during the summer months for all our animals at KNP, and the field data agreed pretty much with conclusions from captive animals, going back to the pioneering work of Prof. C.J. Martin in Melbourne in 1902, that body temperature in Echidnas is highly variable for mammals. To us, following the animals about in their natural habitat, it looked to be a very sensible,

'Servicing' a recording box consisted of changing or turning the cassette tape, which recorded the 'beeps' from the receiver, and delivering fresh batteries. The antenna was placed as high as possible nearby, in this case taped to a dead tree on top of a rocky outcrop.

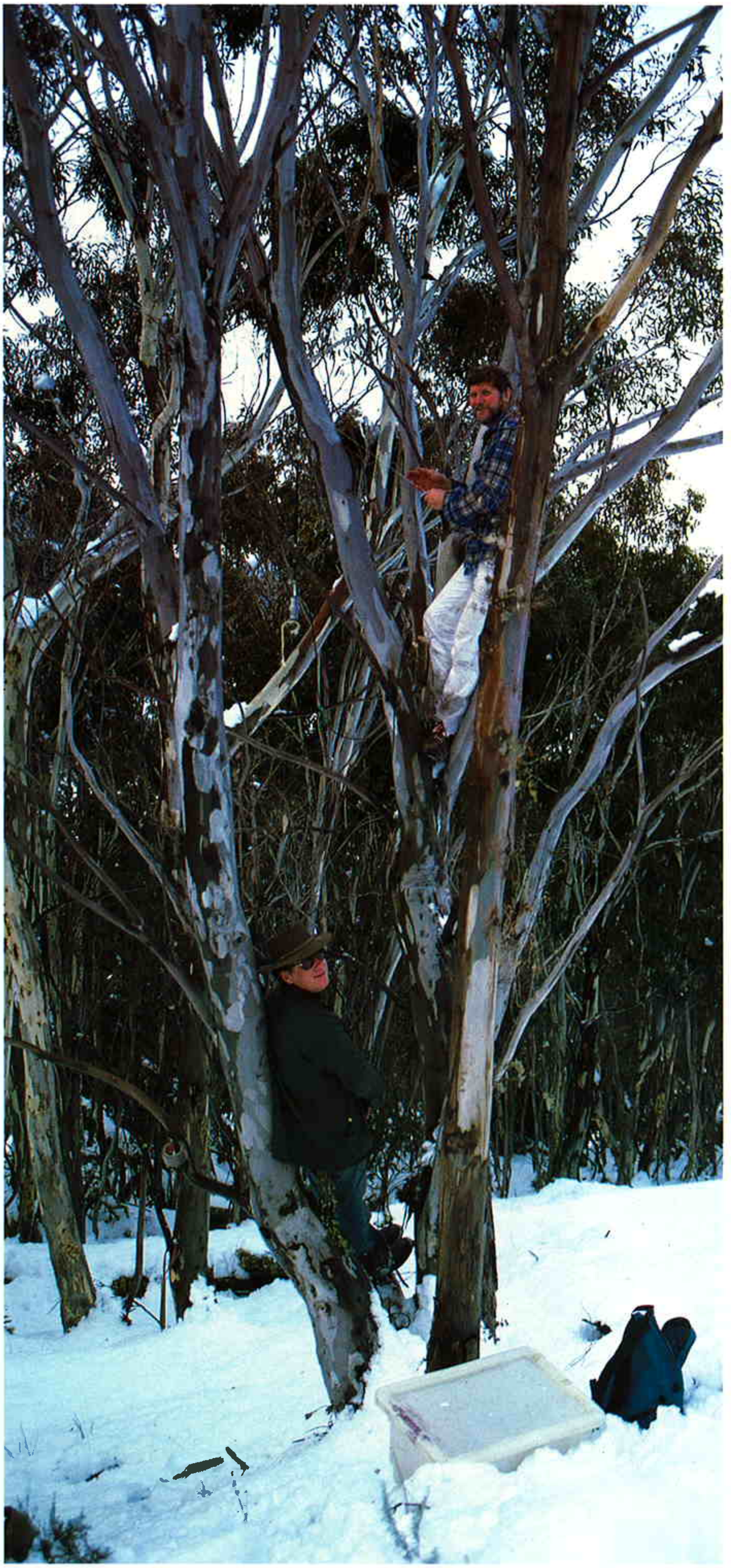
energy-saving pattern, rather than one suggestive of 'poor thermoregulatory abilities' associated with a 'primitive' animal.

We quickly realised how much more data we could obtain (and how much extra sleep we might get!) if we had an automatic sampling system that could gather data overnight. So we invented and deployed a couple of weatherproof systems to record body and ambient temperatures at pre-set times during the night onto cassette tape (see box). It was not until the first apparent 'disaster' in the study that the full potential of these 'boxes' (the system was enclosed in a large polypropylene box) was realised.

At Easter we returned, expecting to turn on the receiver in the vicinity of the last position of an animal and to hear the usual 'beep. . .beep. . .beep' on the appropriate frequency and at the usual rate. Echidnas seemed to have well-established home ranges and were always in the same general area. But when we got together at lunch time Mike Augee, who had gone up to Prussian Plain to locate E10, was pessimistic. He had picked up the signal as expected but it was coming in slowly, with a full 4.5 seconds between beats. That equated to 9.3° C, which was close to ambient temperature, and Mike's gloomy conclusion was that the animal was dead. However, he had not been able to locate the carcass as the long interval between signals made it hard to get a fix. It did seem to be off Prussian Plain, amongst dense snow gum saplings on the steep southern escarpment overlooking the Bullock's Flat ski-tube terminal far below. We discussed the possibilities, including predation (a fox perhaps?) and death from exposure. The first snow had not yet fallen but it had been very cold in the mountains. Maybe the Echidnas in the high country really *were* only strays, at the edge of survival, and this one had just not made the grade.

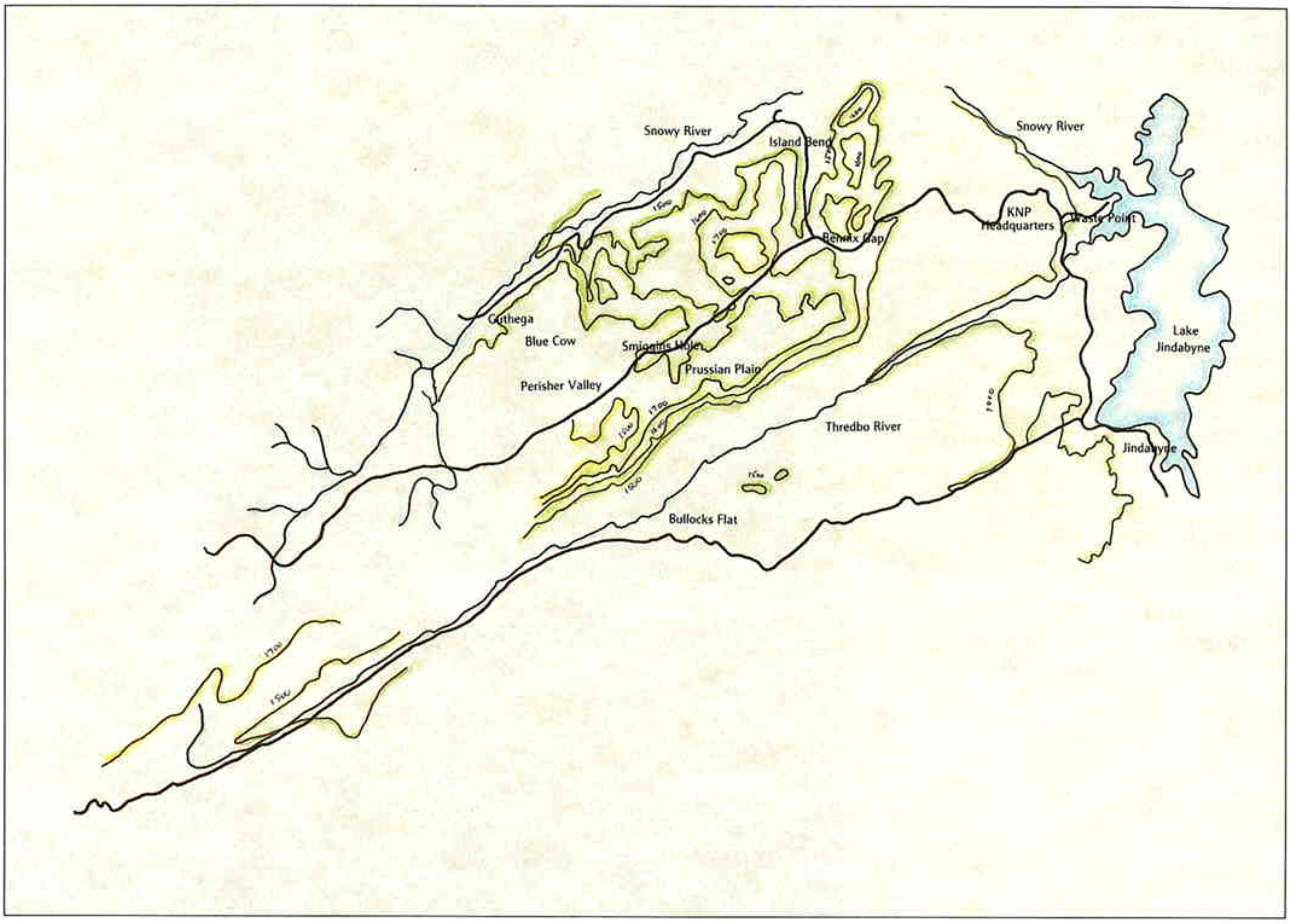
With still a few hours left until nightfall, Grigg set off to Prussian Plain to find E10. It was a quick trip over now familiar terrain to a rock cairn at the southern edge of the plain, overlooking the Thredbo River. After a patient search and a lot of scrambling through thick undergrowth on the precipitous slope, the source of the signal was located under a rock at the base of a large sun-bleached stump. It was typical for an Echidna retreat and there seemed to be every likelihood that E10 had entered there of her own free will. But was she still alive? Telemetry pulses still suggested near-ambient temperature. Perhaps the animal was alive and in torpor?

Here was an exciting problem, but we were committed to leave for Sydney the next day. We needed some way to keep



Gordon Grigg and Mike Augee fix the whip antenna high in a tree so the recording box may still pick up the Echidna's signal if it moves unexpectedly from its hibernation site nearby.

LYN BEARD



CATHY MCGAHEY

Lyn Beard follows a signal from a hibernating Echidna, which was found in a cavity formed between roots of a snow gum under a granite boulder.

GORDON GRIGG

track of the animal's body temperature until we could return. The solution was obvious—set up a 'box' to take readings not hourly or half-hourly, as we had been doing to make overnight records, but every eight hours to spin out the cassette tape for a couple of weeks until our return.

So we climbed again to Prussian Plain early the following morning carrying all the necessary equipment. The sky was blue but it had been damp and cold overnight. On reaching the crest we hurriedly checked the signal. It was more rapid! The animal was now warm! It took only 15.1 seconds for 10 beats, compared to the 45 seconds the previous afternoon. Far from being dead, she had now warmed up. The Echidna story was also hotting up! Periodic and rapid warm-ups from torpor are characteristic of hibernating mammals. Were Echidnas hibernators too? While it was not a sure bet, the odds were changing. We needed more data. We set up the 'box' to record the body temperature every eight hours for the next 15 days and secured the lid down with a large rock (gales are the norm on the Ramshead Range at this time of year).

Fifteen days later in early May we returned and went straight to Prussian Plain. Yes, she was torpid again, and she had moved. But she had moved to the northern side of the ridge out of range of the carefully placed recording box

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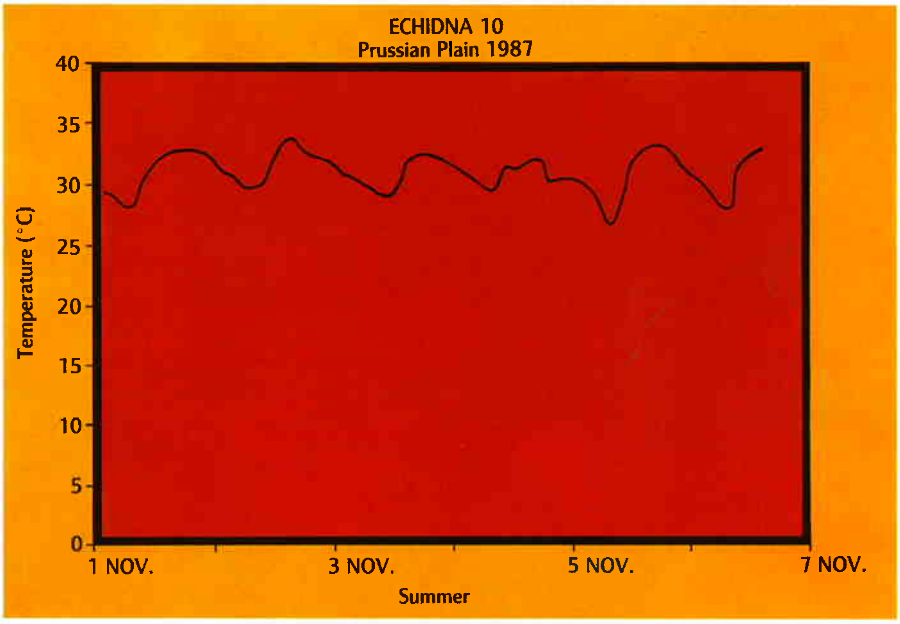
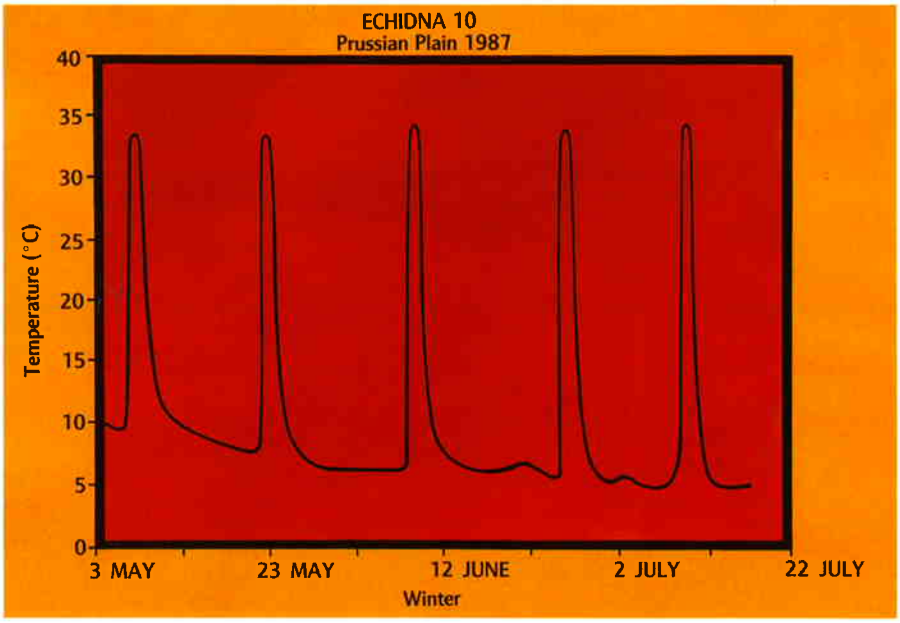
An Echidna (E10) dug up from hibernation is so slow in its movements and so cold that survival seems unlikely.

(Murphy's Law applies especially to field studies!).

Our two other high-country Echidnas, E12 and E15, were also torpid, and so was one of the Echidnas in the 'control' group well below the snowline beside Lake Jindabyne. Torpor was beginning to look like a normal event for Echidnas. Only E13 was still active. The four torpid Echidnas stayed put, with low body temperatures, for the four days of this field trip. We had only two recording boxes, so we left one at the new location of E10 and left the second to record data from another torpid animal. This time we were rewarded for the effort.

On the next trip we listened eagerly to the first tape. It had successfully recorded data every eight hours for two weeks and, most excitingly, it contained in beautiful detail a striking, rapid warm-up over about 12 hours to a 'normal' operating temperature (about 32° C) followed by a slower, steady decline almost to ambient temperature (in this case 10° C). This pattern was to be repeated again and again, every couple of weeks, by *every* monitored Echidna—just what would be expected of a ground squirrel or marmot. Echidnas are hibernators!





IAN FAULKNER

Contrasting patterns in body temperature during summer and winter shown by an Echidna (E10) on Prussian Plain. Note the different time scales. In summer, cyclic changes in body temperature correlate with periods of activity (by day) and rest (at night). In winter the animal entered hibernation in a burrow, its long periods of torpor being interrupted by spontaneous arousals during which body temperatures rose briefly into the low 30s before falling again to near ambient temperature. This pattern of hibernation is the same as that seen in traditional placental hibernators.

A young Echidna discovered in a burrow in a sphagnum bog on Prussian Plain. At 1,720 metres elevation, this is the highest recorded birth of an Echidna and it confirms their ability to cope with the rigours of the alpine climate.

GORDON GRIGG

Hibernation, Torpor, Lethargy or Just Plain Sleep?

At its simplest, hibernation is a vague notion that some animals survive harsh winter conditions by retreating to a den, burrow or nest, not to be seen until spring. Hibernation has often been termed 'winter sleep', in which case awakening should simply be a matter of putting the central nervous system on full alert, a process taking seconds or perhaps minutes. And yet, if you dig up a marmot in winter in the Canadian Rockies, it will take hours to become active, and that arousal will involve a gradual warming with heat produced from the animal's own metabolism until the nervous system is functioning at a normal level. If you dig up a nearby lizard, it will not become active until you apply external heat.

Obviously different vertebrates that remain inactive over winter do so in quite different states. A terminology, with the precision demanded by science, capable of making such distinctions is needed. 'Torpor' is a state in which body temperature is lowered almost to the temperature of the surroundings and functions such as heart beat, breathing and metabolism proceed at rates well below those observed in active animals. 'Hibernation' is used by most zoologists to refer to winter torpor with the additional proviso that the hibernator is capable of completely arousing itself at regular intervals to normal body temperature using its own metabolic resources. This definition therefore excludes all ectotherms and is restricted to birds and mammals. Some small desert birds and mammals show a similar response to summer conditions, in which case the term 'aestivation' is used. What about bears? They are often considered hibernators because they retreat to dens in winter in northern latitudes. In the '50s Raymond Hock, from the Arctic Aeromedical Laboratory in Alaska, measured the body temperatures of a couple of bears in winter in the field and found their body temperatures to be only about 5° C below summer active body temperatures. I have always considered this man, who "made deep rectal insertions" with a thermometer into bears in their dens, to be one of the great field biologists of our time. Needless to say the bears woke up rather quickly and these field measurements have not been repeated since. Most zoologists are content to consider that bears, like skunks and a few members of the order Carnivora, exhibit 'carnivorean lethargy'.

Hibernation involves complex seasonal cycles. Few mammalian hibernators are able to enter torpor during the summer active period. The reproductive season appears to require physiological conditions that preclude torpor. Many bats, however, can enter torpor at any time of the year. There are therefore a number of variations in the way different species utilise torpor. This has led to continuing adjustment of the terms used above and a search for a more quantitative definition of hibernation. Since mitochondrial membranes (which produce energy for many cell functions) of most endotherms cannot function at temperatures below 18° C, with the exception of those of hibernators, it is possible to define hibernators as those endotherms capable of lowering the minimal temperature of membrane function below 15° C. By this definition bears are not hibernators but Echidnas are.

—M.L. Augee

Hibernation: Primitive or Advanced?

Australian biologists are a bit touchy about the word 'primitive'. It is often applied to our native species, such as marsupials and especially monotremes. That implies they are second-class animals, isolated on a geographic ark and doomed to be out-competed by 'advanced' mammals from the 'real' world over the seas. The problem is that 'primitive' carries two meanings that are not necessarily compatible. It carried in biology the meaning of 'ancestral' in the case of phylogeny and 'old' in terms of the fossil record. It also of course means lacking in complexity, which has implications of being inefficient and old-fashioned. To get around this, a new word 'plesiomorphic' has been coined to carry the meaning 'ancestral' only.

Hibernation was originally considered primitive. Small mammals were said to 'abandon homeothermy' and revert during winter to a reptilian metabolism. Mammalian hibernation was considered to be a remnant of reptilian physiology held in a few mammals. In other words, it was then held to be a 'plesiomorphic' character state. In recent times, however, hibernation has come to be considered a very advanced ability, involving seasonal adjustment of function and even structure in the case of some membranes. Since hibernators are found in at least four separate orders, if hibernation is an advanced state it would have to have evolved separately at least four times. In evolutionary terms this would be an example of four-fold convergence. And now we have evidence that Echidnas hibernate. That should shift the balance toward the older view, since monotremes are the closest living mammals to the Mesozoic stem. Otherwise we are faced with five-fold convergence of a quite complicated character state, and that stretches the concept a bit too far. Obviously more information is needed about the basis of hibernation in the Echidna, and it could be that evolutionary terms and concepts that fit structural characters so well cannot be applied to functional states.

—M.L. Augee

The strategy of hibernating and conserving energy during the period of the year when food may be in short supply or when environmental conditions are harsh makes sense in one of the coldest areas of Australia. However, there remains the problem that Echidnas are supposed to breed in July or early August. At first it looked as though they were indeed going to hibernate through the breeding season, and some did, but with a further year of monitoring we confirmed that most of them aroused in time for mating and breeding. The other animal being studied on Prussian Plain, E12, in fact hatched a living young in a burrow dug in a clump of sedge and sphagnum, providing strong evidence that the high-country Echidnas really live in that habitat and are not simply occasional visitors that become 'lost'.

To what extent hibernation in Echidnas is homologous to that of eutherian (placental) hibernators is still uncertain. The pattern is the same, but we do not know whether it is supported by the same physiology. If monotreme and eutherian hibernation are homologous, then this is a bit hard to reconcile with the current idea that hibernation is an advanced state derived in only a few mammals. Perhaps monotreme hibernation is based on physiological mechanisms present in ancestors common to all mammals, in which case further studies of thermoregulation in Echidnas might shed light on the development of endothermy and homeothermy in metatherian (marsupial) and eutherian mammals. Either way, the discovery of hibernation in Echidnas poses some questions for the old debate on whether hibernation is a primitive or advanced character state (see box). It also poses interesting questions about Echidnas themselves. How widespread is the occurrence of torpor, and is the ability to become torpid used under completely different circumstances in other areas?

The discovery of hibernation in Echidnas, like the recent discovery of electrosensitivity in monotremes (see ANH vol. 23, no. 4, 1990), indicates there is still much to be discovered about these fascinating beasts. All of which serves to reinforce Mike Augee's oft-quoted maxim "Never underestimate an Echidna!". ■

Suggested Reading

Grigg, G.C., Beard, L.A. & Augee, M.L., 1989. Hibernation in a monotreme, the Echidna (*Tachyglossus aculeatus*). *Comp. Biochem. Physiol.* 92A: 609–612.

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